




## Article

# Functional Trait Responses of C4 Bunchgrasses to Fire Return Intervals in the Semi-Arid Savanna of South Africa

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**Abstract:** C4 grasses coevolved with fires, employing specialized adaptive traits to recover from recurrent fires of varying regimes, thereby maintaining plant diversity and plant population stability. However, the knowledge of how C4 bunchgrasses recover from varying fire return intervals (FRIs) is limited. Biomass, tillering, flowering, and growth-related traits of *Digitaria eriantha*, *Themeda triandra*, *Sporobolus fimbriatus*, and *Cymbopogon plurinodis* were assessed in 0- (unburned), 1-, 2-, and 4-year FRIs, each applied in two  $0.5 \pm 0.01$  ha plots from 1980–2022 at the University of Fort Hare research farm, South Africa. FRIs and grass species interacted significantly on biomass production, crown size, tiller production, and reproductive tillers, with responses varying interspecifically depending on the FRI. *Cymbopogon plurinodis* attained higher total biomass in 1-year FRI, whereas *T. triandra* produced relatively low biomass in all FRIs compared to 0-year FRI. Nonetheless, *T. triandra* attained nearly two to three-fold more tillers per plant and three to five-fold more reproductive tillers in 2- and 4-year FRIs compared to other FRIs. Similarly, *S. fimbriatus* had two-fold more reproductive tillers in 2-year FRIs compared to 0- and 1-year FRIs. We deduce that C4 bunchgrasses respond differentially under recurrent fires depending on the fire return interval, with 2- and 4-year FRIs promoting vegetative and sexual regeneration by enhancing tillering and flowering.

**Keywords:** fire frequencies; grasses; biomass; tiller production; flowering; growth-related traits; South Africa



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## 1. Introduction

Dating back to the Miocene age, fires have been an integral part of global ecosystems, shaping vegetation structure and sustaining ecosystem services [1,2]. Currently, fire is used as a vegetation management tool to prevent the proliferation and establishment of woody plants and to improve herbaceous plant diversity, productivity, and quality [2,3]. The recovery potential of herbaceous plants to fires, however, varies widely depending on the fire adaptive strategies, amongst others, recruitment from the seed or regeneration from clonal organs [4]. These post-fire recovery strategies are dependent on flowering and bud production, as these traits determine the number of seeds and tillers produced following fires [2]. However, although these reproductive and clonal traits co-occur in grasses, they exhibit a trade-off in which one trait is sacrificed for another. Apart from these

traits, productivity traits, including biomass production, have long been used to assess plant responses to fire [4].

Perennial C4 grasses have evolved several times under recurrent fires of varying regimes; hence, they remain persistent in fire-prone ecosystems [5]. Recent evidence by Moore et al. [6], based on 52 grass species responses to fire, indicated that C4 species are more resilient to fires relative to C3 grasses. Post-fire recovery of C4 grasses is facilitated mainly by their large below-ground carbohydrate reserves, vigorous root system, and higher nitrogen use efficiency [7]. These fire recovery mechanisms facilitate fast and vigorous bud regeneration and the initiation of new phytomers, thereby increasing tiller densities and biomass [8]. However, the post-fire recovery potential of grasses depends largely on the extent to which plant meristems were exposed to fires [9].

Generally, below-ground resprouters are safe from fires, while above-ground crown resprouters, e.g., bunchgrasses, are perceived to be at risk because their apical meristems are elevated to the flame heights of surface fires [10–12]. Conversely, creepers, largely rhizomatous species, are insulated by soil against fires, which limits damage to their meristems [13]. However, it remains unanswered why bunchgrasses, which resprout from the crown, remain persistent in fire-prone ecosystems. While attempts have been made to answer this question by Simpson et al. [4] in the semi-arid savanna of South Africa, the study was limited to one fire frequency, which limits understanding of how various grass species respond to varying fire regimes. Generally, different grasses respond interspecifically to fire, depending largely on the fire return intervals (FRIs), as certain FRIs select for specific plant adaptive traits related to post-fire persistence and recovery [14,15]. Short FRIs, in particular, reduce plant fitness and survival, causing the extinction of fire-intolerant species, leading to the loss of plant diversity and a decline in biomass productivity [4]. Frequent fires cause serious damage to plants without allowing adequate recovery, owing to the depletion of carbohydrate reserves and limited bud regeneration, which reduces plant resilience to fires [10]. Nonetheless, a knowledge gap still exists regarding how different C4 bunchgrasses respond to varying FRIs. As a result, the appropriate FRI that can promote resprouting, growth, productivity, and flowering of grasses is yet to be ascertained in South African savanna ecosystems. This information is critical, given that future climate change characterized by erratic rainfall and extremely high temperatures is projected to increase fire frequencies and extend the length of the burning season [16,17]. Understanding the functional trait responses of bunchgrasses to varying FRIs provides insights into post-fire plant recovery and persistence strategies to inform biodiversity conservation and the formulation of appropriate fire management prescriptions for local land users. This study, therefore, used a long-term fire experiment initiated 43 years ago to assess the effects of varying fire return intervals on grass functional traits related to growth, productivity, and reproduction. Additionally, we assessed the relationships between grass functional traits. We answered the following questions: (1) how do different C4 bunchgrasses respond along a gradient of fire return intervals? and (2) what are the relationships between functional traits of bunchgrasses subjected to recurrent fires?

## 2. Materials and Methods

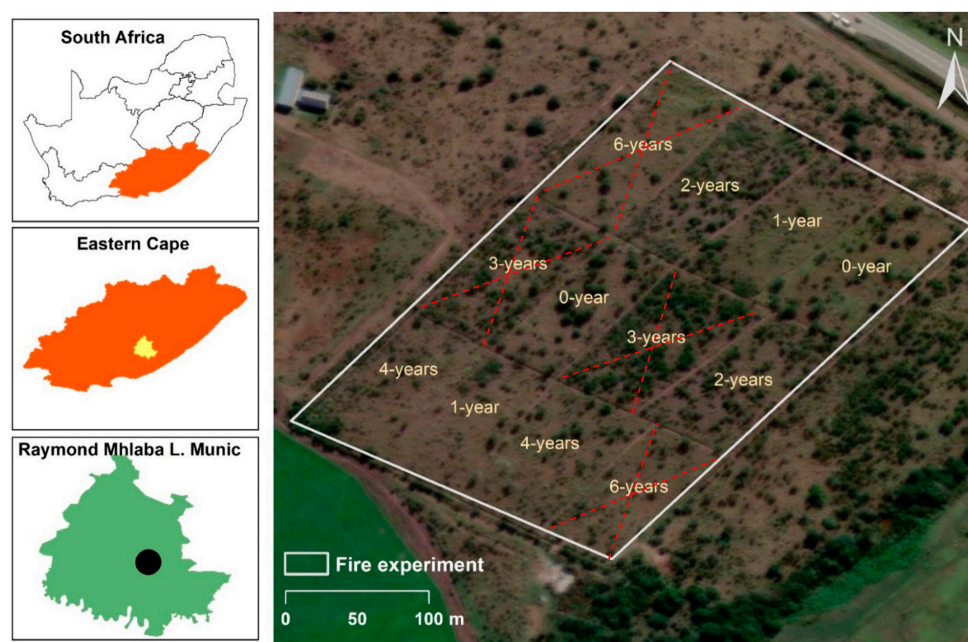
### 2.1. Study Area

This research was conducted in a long-term fire trial that was established in 1980 at the University of Fort Hare research farm in Alice (32°47' S and 26°52' E) under Raymond Mhlaba municipality, Eastern Cape Province of South Africa. The climate of the study area is semi-arid, with a long-term rainfall of 500 mm per year [18], and the temperatures range from 4 °C in July to 28 °C in February [19]. The main rainy season commences around October and ends around March, with 70% of rainfall being distributed across this period [18]. The vegetation type of the study area is Bisho thornveld, found in a semi-arid savanna biome, with *Vachelia karoo* dominating a mixed woody landscape [20]. The herbaceous vegetation is dominated by the following C4 perennial bunchgrasses: *Themeda triandra*, *Digitaria eriantha*, *Sporobolus fimbriatus*, *Cymbopogon plurinodis*, and *Eragrostis* species. The ex-

perimental site is characterized by silty loam soils of the Glenrosa form or Ochric Cambisols, with the top horizon being stony [21].

## 2.2. Experimental Design and Layout

At the initiation of the experiment, trees were removed using cut-stump treatment [22], and all plots were burned for the first time in August 1980 to ensure uniformity of vegetation and soils across the plots [18]. Thereafter, fire was applied at different intervals to make the following fire frequencies: unburned, annual, biennial, triennial, quadrennial, and sexennial burns corresponding to 0-, 1-, 2-, 3-, 4-, and 6-year fire return intervals (FRIs). However, the 3- and 6-year FRIs were excluded in this study because they were not burned in the same year as other FRIs, as their inclusion would potentially cause variation in time since last fire (TSF) between these FRIs. The fire is normally ignited during the spring, around August, just after the first rains, to manage herbaceous vegetation composition. The fire was applied when air temperatures and humidity were on average 23 °C and 52%, respectively, to avoid high-intensity fires that would cause severe damage to herbaceous plants. The wind speed for the last fire application varied temporarily with time between 15 and 18 km/h, with fires burning for 5 to 7 min in each plot. The fuel load was on average 4989.0, 4459.2, 3473.0, and 4560.7 kg/ha in 0-, 1-, 2-, and 4-year FRIs, respectively, during the last fire application. The last fires were applied in August 2022 for all fire frequencies except for 3- and 6-year FRIs, which were both excluded in this study (Figure 1). Fire ignition was conducted using a drip torch filled with diesel and petrol at a 60:40% ratio. The head fires were applied, in which fire was ignited in the direction of wind through the quick pulling of a drip torch along the periphery of the plot.



**Figure 1.** The maps of the study area (on the left) and the layout of the experiment of fire return intervals (on the right) were initiated in 1980 at Raymond Mhlaba L. municipality in Alice, Eastern Cape, South Africa. The black dot indicates the experimental site, and Munic means municipality. 0-year = unburned, 1-year = burned once every year, 2-years = burned every second year, 3-years = burned every third year, 4-years = burned every fourth year, and 6-years = burned every sixth year. The crosses (x) in the 3- and 6-year FRI indicate that these FRI treatments were not included in this study.

Each FRI was replicated two times in a completely randomized design, with each replicate measuring  $0.5 \pm 0.01$  ha in size and interspaced by a 5 m border. Two controls of similar size as FRI plots have remained unburned since the initiation of the experiment

(Figure 1). In each replicate plot, a 100 m line transect was delineated across the center. Four 10 × 10 m subplots were marked at 20, 40, 60, and 80 m along the transect, within which grass species were sampled.

### 2.3. Species and Data Collection

Sampling was conducted on 15 February 2023 during peak production and flowering. Four C4 perennial bunchgrasses dominant in all FRIs were selected. The selected species were *Themeda triandra*, *Digitaria eriantha*, *Sporobolus fimbriatus*, and *Cymbopogon plurinodis* (Figure S1). Although these species vary in terms of grazing value [23], all of them play a crucial role in grazing. The latter two species are regarded as low-quality grasses, but, in the absence of the highly nutritious species, they form a large part of the ruminant diet in the semi-arid savannas of South Africa [23]. We assessed several functional traits related to the growth (height, crown area, and canopy cover), tillering (total number of tillers), productivity (leaf, tiller, and total biomass), and flowering (number of reproductive tillers) of these grass species. A 1 m<sup>2</sup> quadrat was placed at the center of each 10 × 10 m subplot, and an individual of each species was sampled ( $n = 8$  plants per species per treatment), totaling 160 plants. If the plant for a particular species was not encountered in the quadrat, the individual plant nearest to the quadrat within the 10 m radius was selected. The height, canopy diameter, and crown diameters (east-west and north-south) were measured using a standard ruler. The canopy diameter was measured at a leaf table height [24], whereas the height was measured from the base to the tip of the primary tiller. Thereafter, each plant was cut at a stubble height of 5 cm and placed in separate paper bags. Each bag containing grass biomass was weighed and emptied, and the biomass was separated into tiller and leaf fractions. The leaves were detached with sheaths. From each individual plant, the total number of tillers was counted, and the reproductive tillers were determined. A tiller was considered reproductive if the spikelets contained visible florets; otherwise, if no florets were noticeable, we considered that tiller to be aborted because sampling was conducted during peak flowering. Plant biomass was oven-dried at 75 °C for 48 h, after which each sample was weighed to determine dry matter production. Tiller and leaf biomass were weighed separately and later added to determine the total biomass. The crown area was computed using the area of a circle.

### 2.4. Statistical Analysis

The data normality and homogeneity of variance were first assessed using Kolmogorov-Smirnov and Levene's tests, respectively. The Q-Q plots and density plots were used to visualize data dispersion. For parameters, e.g., biomass and reproductive tillers, which did not meet the assumptions of ANOVA, we applied  $\log_{10}(x + 1)$  and square root transformations to normalize the data. However, the means ( $\bar{x}$ ) and their associated standard errors (SEMs) were later backtransformed to the original scale. ANOVA was conducted to assess the fixed effects of fire return intervals ( $n = 4$ ) and species ( $n = 4$ ) and their interactions on grass functional traits using general linear models (GLMs) in Jamovi 2.3, the graphical interface of R. The GLM models were expressed as follows:

$$Y_{ijk} = \mu + T_i + S_j + TS_{ij} + \varepsilon_{ijk}$$

where  $Y$  = plant functional trait (biomass, tiller numbers, reproductive tillers, canopy diameter, and crown area),  $\mu$  = mean,  $T_i$  = effect of the  $i$ th fire return intervals (FRIs),  $S_j$  = effect of the  $j$ th species,  $TS_{ij}$  = effect of the interaction of the  $i$ th FRIs and  $j$ th species, and  $\varepsilon$  = random error.

Due to low replication, analysis was conducted at the plant level, with each sampling point for each individual plant nested within each replicate plot ( $n = 4$  per plot). The significance of the models was tested using an F-test at a 95% confidence level. The mean comparisons between fire return intervals were conducted using Tukey's test. The Holm adjustment method was applied to generate Pearson's correlations ( $r$ ) to determine bivariate relationships between grass functional traits.



### 3. Results

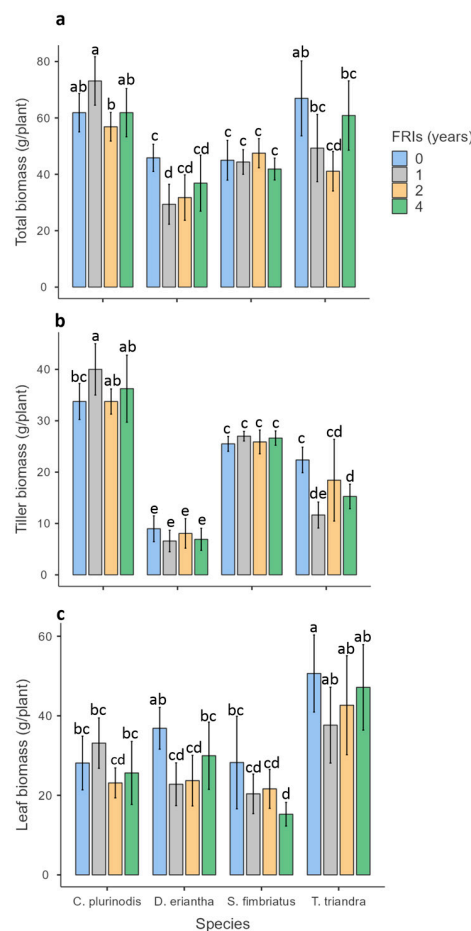
#### 3.1. Biomass Production

Fire return intervals (FRIs) and grass species interacted significantly for above-ground total biomass ( $F_{9,128} = 1.09, p = 0.027$ ) and tiller biomass ( $F_{9,128} = 0.84, p = 0.003$ ; Table 1). The biomass responses to FRIs were largely interspecific ( $p < 0.001$ ), with *C. plurinodis* attaining significantly higher above-ground total biomass (ATB) in a 1-year FRI compared to a 2-year FRI (Figure 2a). Conversely, ATB of *T. triandra* was negatively affected by fire in 2-year FRIs compared to 0- and 4-year FRIs, with 0-, 1-, and 4-year FRIs exhibiting similar biomass (Figure 2a). The ATB of *D. eriantha* and *S. fimbriatus* remained similar from 0- to 4-year FRIs (Figure 2a).

**Table 1.** ANOVA results showing the effect of species, FRIs, and their interactions on plant functional traits of bunchgrasses.

SOV	DF	ATB		TB		LB		TT		RT		CA		CD		HT	
		F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Spp	3	5.00	<b>0.003</b>	42.71	<b>&lt;0.001</b>	0.73	<b>&lt;0.001</b>	45.75	<b>&lt;0.022</b>	14.1	<b>&lt;0.001</b>	6.77	<b>&lt;0.01</b>	44.6	<b>&lt;0.001</b>	<b>2.84</b>	<b>&lt;0.001</b>
FRI	3	3.84	<b>0.006</b>	18.88	<b>&lt;0.001</b>	6.40	0.537	3.34	<b>&lt;0.001</b>	7.99	<b>&lt;0.001</b>	0.83	0.481	1.05	0.384	0.69	0.557
Spp * FRI	9	1.09	<b>0.027</b>	0.84	<b>0.003</b>	0.51	0.863	1.84	<b>0.050</b>	2.24	<b>0.025</b>	0.63	0.770	2.76	<b>0.047</b>	0.34	0.960

Spp = species, FRI = fire return interval, CD = canopy diameter, CA = crown area, ATB = above-ground total biomass, TB = tiller biomass, LB = leaf biomass, TT = total tillers, RT = reproductive tillers, HT = height. SOV = source of variation, DF = degrees of freedom, F = F-value, p = p-value. Bold p-values indicate significant effects at  $p < 0.05$ . The \*sign indicates the interaction between Spp and FRI.

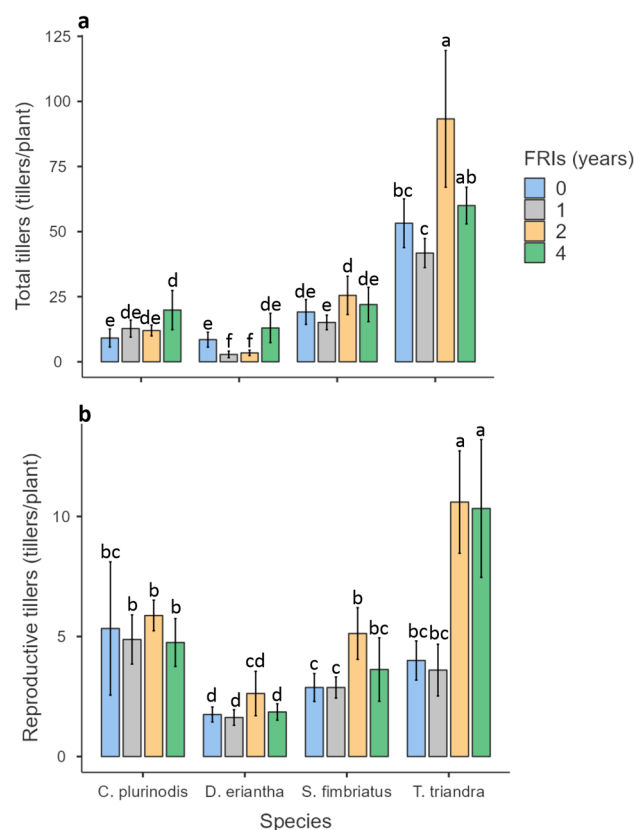


**Figure 2.** Above-ground total biomass (a), tiller (b), and leaf biomass production (c) of four bunchgrasses across different fire return intervals. The 0-year fire return interval denotes unburned plots. Bars indicate means, and error bars indicate standard errors. Different superscripts between two bars denote significant differences at  $p < 0.05$ .

The tiller biomass (TB) was consistently similar from 0- to 4-year FRIs for *C. plurinodis* and *S. fimbriatus* (Figure 2b). The leaf biomass (LB) was neither affected by the FRIs ( $p = 0.537$ ) nor by the interaction between species and FRIs ( $p = 0.863$ ; Table 1). LB varied largely by species ( $p < 0.001$ ), with *T. triandra* having a higher LB than *D. eriantha* and *S. fimbriatus* (Figure 2c).

### 3.2. Tiller Production

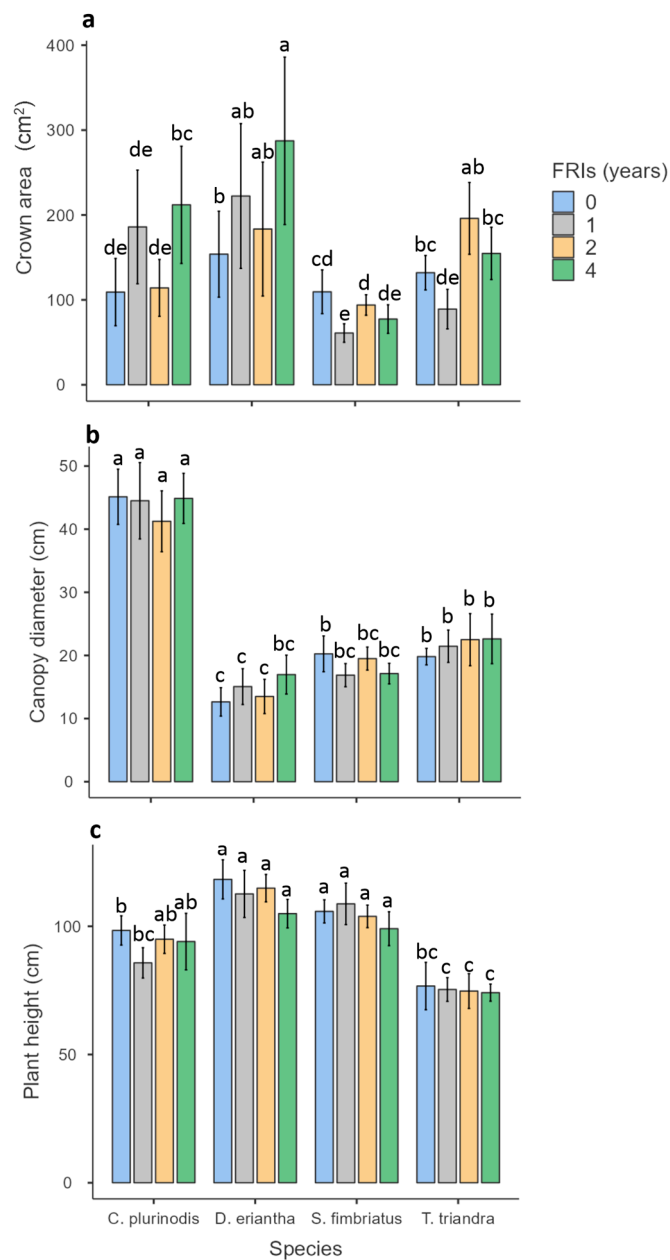
The species-by-FRIs interactions were significant for total tiller production ( $F_{9,128} = 1.84$ ,  $p = 0.050$ ) and reproductive tillers ( $F_{9,128} = 2.24$ ,  $p = 0.025$ ; Table 1). *Themeda triandra* attained nearly two to three-fold more tillers per plant in 2-year FRIs compared to 0, and 1-year FRIs, whereas the reproductive tillers were three-fold higher in both 2- and 4-year FRIs than other FRIs (Figure 3a,b). The 2-year FRI had more tillers per plant than the 1-year FRI and two-fold more reproductive tillers than the 0 and 1-year FRIs for *S. fimbriatus* (Figure 3a,b). Similarly, tiller production of *C. plurinodis* in 4-year FRIs doubled that in the 0-year FRIs, but the reproductive tillers were similar across all FRIs (Figure 3a,b).



**Figure 3.** Total tiller production (a) and reproductive tillers (b) of four bunchgrasses across different fire return intervals. The 0-year fire return interval denotes unburned plots. Bars indicate means, and error bars indicate standard errors. Different superscripts between two bars denote significant differences at  $p < 0.05$ .

### 3.3. Canopy and Crown Size

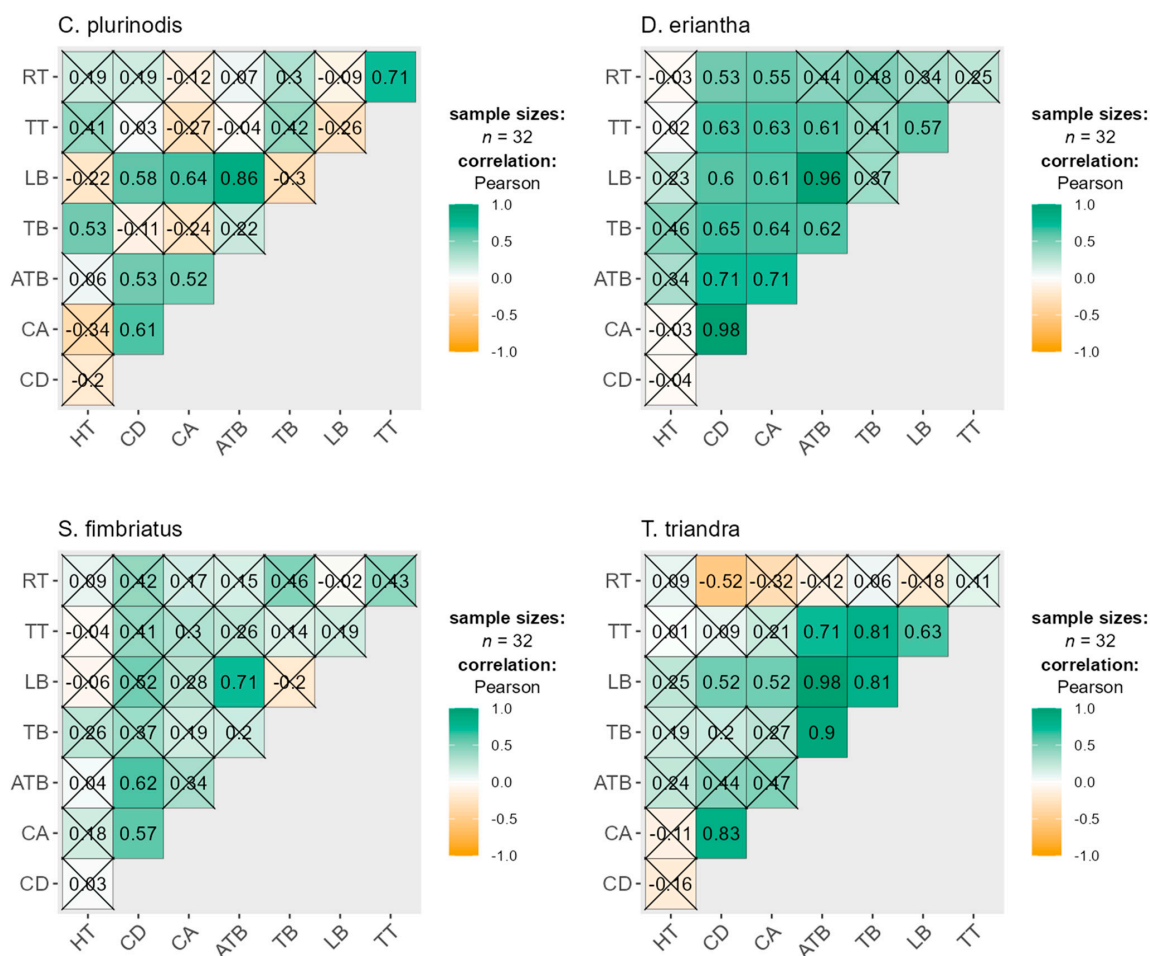
Canopy area (CA) and plant height were not affected by FRIs and interactions between species and FRIs ( $p > 0.05$ ) but varied significantly by species (Table 1; Figure 4b). However, FRIs and species interacted significantly ( $F_{9,128} = 2.76$ ,  $p = 0.047$ ) for canopy diameter (Table 1). *Cymbopogon plurinodis* had twice as much CD as other species from 0- to 4-year FRIs (Figure 4a). However, there were no significant differences on the CD of *C. plurinodis* from 0- to 4-year FRIs. The CD of *D. eriantha*, *S. fimbriatus*, and *T. triandra* was consistently similar across the FRIs (Figure 4a).



**Figure 4.** The crown area (a), canopy diameter (b), and plant height (c) of the bunchgrasses across different fire return intervals. The 0-year fire return interval denotes unburned plots. Bars indicate means, and error bars indicate standard errors. Different superscripts between two bars denote significant differences at  $p < 0.05$ .

### 3.4. Relationships between Functional Traits

For all grass species, above-ground total biomass (ATB) correlated largely with leaf biomass ( $r = 0.71\text{--}0.98$ ,  $p < 0.001$ ; Figure 5). Furthermore, ATB also increased with canopy size for *C. plurinodis* ( $r = 0.53$ ,  $p < 0.001$ ), *D. eriantha* ( $r = 0.65$ ,  $p < 0.001$ ), and *S. fimbriatus* ( $r = 0.62$ ,  $p < 0.001$ ). Likewise, ATB correlated positively ( $r = 0.64\text{--}0.71$ ,  $p < 0.01$ ) with crown area for *C. plurinodis* and *D. eriantha*. Moreover, there was a clear positive correlation between ATB and tiller biomass (TB) for *D. eriantha* and *T. triandra* ( $r = 0.62\text{--}0.90$ ,  $p < 0.05$ ; Figure 5). The leaf biomass increased with tiller production for *D. eriantha* ( $r = 0.57$ ,  $p = 0.003$ ) and *T. triandra* ( $r = 0.63$ ,  $p < 0.001$ ). The plant height was unrelated ( $p > 0.05$ ) to other plant functional traits for all species except *C. plurinodis* (Figure 5).



**Figure 5.** Pearson correlations between plant functional traits of different bunchgrasses. HT = height, CD = canopy diameter, CA = crown area, ATB = above-ground total biomass, TB = tiller biomass, LB = leaf biomass, TT = total tillers, RT = reproductive tillers. The cross (x) in boxes denotes a non-significant Pearson (r) correlation ( $p > 0.05$ ) between two parameters.

#### 4. Discussion

##### 4.1. Effect of Varying Fire Return Intervals on Grass Biomass Production

The results of this study show that biomass production and tillering of C4 grass species respond interspecifically to fire, depending on the fire return intervals. Specifically, the significant interactions between FRIs and species suggest that plant recovery from recurrent fires depends not only on fire frequency but also on species-specific tolerance to certain fire regimes. Generally, the storage reserves, root biomass, and efficient use of growth resources vary by species type; hence, the post-fire recovery potential of grasses differs by species [7]. In this study, biomass production of *C. plurinodis* responded positively to short fire return intervals, more so annual fires, while the opposite was true for *T. triandra* (Figure 2a). High regeneration of *Cymbopogon plurinodis* in frequently burned plots could be attributed to the fact that, unlike *T. triandra*, *Cymbopogon* species invest more biomass in root production in fire-prone areas, which enhances their vigorous recovery following fires [4]. High below-ground investment enhances higher resource uptake and carbohydrate storage, which together facilitate faster regeneration, a higher photosynthetic rate, and biomass production [7]. These results suggest that under future climate scenarios when fire return intervals are short, the forage will be constituted mainly by less palatable *C. plurinodis*, leading to reduced herbivore diet quality. In this study, biomass production was explained largely by leaf biomass (Figure 5), highlighting that biomass production of these C4 grasses depends largely on resource investment in leaf production. Generally, C4 grasses respond



to fires through increased leaf replacement and the development of new phytomers [10]. However, although tiller biomass was similar between unburned and other FRIs, the tiller numbers were lower in the former (Figure 2a), indicating that tiller biomass depended not only on tiller numbers but also the sizes. Apparently, the 1-year FRI reduced tiller biomass compared to unburned controls for *T. triandra* and leaf biomass for *D. eriantha* (Figure 2b). Too-frequent fires, e.g., 1-year FRI, are detrimental to plant regeneration [25], particularly resprouting, due largely to short intervals between burns that do not allow adequate regrowth of plant buds, in turn minimizing their contribution to biomass [11]. This could be ascribed to the limited replenishment of carbohydrate reserves and meristematic tissues under these frequent burns, which restrict the replacement of dead buds with new ones [10].

#### 4.2. Effect of Fire Return Intervals on Tillering, Crown Size, and Flowering

Tiller production was lowest in the 1-year FRI compared to other FRIs (Figure 3a). These findings, however, disagree with those of Benson [26], who recorded more tiller buds in the annual burned scenario relative to the unburned scenario. The differences between our findings and Benson [26] could be explained by the fact that the latter assessed rhizomatous species that are insulated by soils against fire [27], whereas this study tested bunchgrasses whose meristems are exposed to fires. The 2-year FRI, particularly, enhanced tiller production for all species relative to the 1-year FRI, despite the fact that the effects were not significant for *D. eriantha* and *C. plurinodis* (Figure 3a). Similarly, 2-year FRI facilitated grass recovery in the study by Rowe [28]. In the 1-year FRI, the crowns of grasses were more exposed to fire due to the low clumping of tillers caused by repeated burns, while in other FRIs, the tiller clumping prevented combustion of some tillers. The reduction in crown area in 1-year FRI was more apparent in *T. triandra* and *S. fimbriatus* (Figure 4b), which could be ascribed to higher dead material in their bases, which probably fueled intense fires, which in turn depleted basal tillering. As a result, tiller production in almost all species did not translate to an increase in crown area, as indicated by non-existent or negative correlations between tiller production and crown area (Figure 5). These findings indicate that basal tillering contributed minimally to crown size, largely due to aerial tillering. Thus, these species are more vulnerable to fires, as aerial tillers are more exposed to fire flames than basal tillers [10,12].

Our results further show that 2-year FRI also stimulated flowering (Figure 3b), as indicated by higher reproductive tillers compared to other FRIs, particularly for *T. triandra* and *S. fimbriatus*. This indicates that the population maintenance of these grass species following fires does not rely only on vegetative tiller recruitment but also on the recruitment of new individuals from seeds. The increase in flowering following fires was also reported by Simpson et al. [4] for most of the species studied here and by Ellsworth and Kauffman [29] for other C4 grasses elsewhere. However, the results of this study show that, unlike Simpson et al. [4], increased flowering was more apparent in 2- and 4-year FRIs than in 1-year FRIs. Generally, the reproductive maturity of *T. triandra* is attained in the second year of the plant's life; hence, burning every year interrupts its reproductive cycle, thereby limiting flowering [30]. Thus, burning early in the spring every 2–4 years affords *T. triandra* adequate time to produce reproductive tillers [31]. In agreement with our findings, Morgan and Lunt [32] also found that in Australian grasslands, *T. triandra* required FRIs of at least 2–4 years to sustain its high tillering. Fire application every 2–4 years may be more significant for plant population maintenance, habitat management, and diversity conservation. Generally, maintaining *T. triandra* populations through the application of these FRIs could be more beneficial for game and livestock production due to their high grazing value.

The negative relationships between tiller production and plant height signify that investing in primary stem growth limits grass tillering. These findings support the theory of apical dominance, in which the growth of the primary tiller dominates, restricting the emergence of new axillary buds [33]. However, we lack tangible evidence to support this view; therefore, future research to advance the knowledge of the effect of plant dominance

on the emergence of new buds under different fire return intervals is recommended. It was, however, not surprising that the reproductive tillers were negatively or unrelated to growth and biomass-related traits (Figure 5) because growth is limited during flowering as more resources are channeled to reproduction.

## 5. Conclusions and Recommendations

The results of the study showed that the productivity, crown size, and tiller production, including reproductive tillers, of C4 bunchgrasses are interspecific, depending largely on the fire return intervals (FRIs). These results suggest that C4 bunchgrasses evolved differentially under recurrent fires of different return intervals, signifying that the persistence of bunchgrasses depends on the fire regime type. The 2- and 4-year FRIs, for instance, promoted higher tiller production and flowering of *T. triandra* and *S. fimbriatus*, indicating that the population persistence of these species is promoted by these FRIs through both vegetative regeneration and recruitment from the seeds. Thus, the timing of fire application, particularly burning every 2–4 years, is recommended for land users. On the other hand, annual burns proved to be detrimental to plant recovery by reducing tillering and flowering of the C4 grass species, signifying a need to prevent annual fires. Our findings provide a mechanistic understanding of the post-fire recovery dynamics of C4 bunchgrasses and are a basis for future fire management and policymaking in the semi-arid savannas of southern Africa.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15121201/s1>, Figure S1: The bunchgrass species assessed for functional traits responses to fire return intervals. A = *Themeda triandra*, B = *Cymbopogon plurinodis*, C = *Sporobolus fimbriatus* and D = *Digitaria eriantha*.

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